

**Ground based LiDAR demonstrates the legacy of
management history to canopy structure and composition
across a fragmented temperate woodland**

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Running head: Canopy structure of managed forests

25 **Abstract**

26 The structure of forest canopies correlates with stand maturity and biomass, and
27 develops consistently over time. Remote-sensing technologies such as Light Detection
28 and Ranging (LiDAR) have become prominent tools for measuring structural
29 characteristics of forests.

30 We walked a portable canopy LiDAR (PCL), an up-facing rangefinder that detects
31 vegetation through the canopy at two kilohertz, along multiple transects at ten
32 different forest stands in the area of Wytham Woods, Oxfordshire, UK. The stands
33 had different species composition, were situated at forest edges and in forest core,
34 were in fragments of different sizes and had different land-use histories. With these
35 data we tested structural differences in vegetation across these stand types.

36 Although none of the stands have been managed in the last 70 years, they have not
37 converged structurally. Vertical canopy structure differed between stands that regrew
38 naturally from open field and those with a history of coppice management. Forest
39 stands that have developed following major fellings or through spread on to former
40 grazing land showed some structural similarities to classic natural succession from
41 large disturbances. Stands that were actively managed as coppice over preceding
42 centuries, showed a similar structural pattern to mature forest, but without the tall
43 overstorey that can develop into old growth communities.

44 This structural divergence indicates two distinct pathways for secondary forests: with
45 implications for the future biomass, stand structure, and species composition. The
46 legacy of management practices can determine canopy structure decades after the
47 forest is removed from active management, but can also be difficult to discern with
48 remote sensing data. We recommend that “ground-truthing” remote sensing data go
49 beyond traditional checks of height and topography, as the history and composition of
50 secondary forests can have an important influence on the pace and compositional
51 structure of recovery from management.

52

53 *Keywords: Canopy structure, LiDAR, Forest fragments, Land-use history, Disturbance.*

54 **1. Introduction**

55 Tree canopies exert strong influences on the structure and function of forest
56 ecosystems (Lowman and Rinker, 2004; Shugart et al., 2010). Spatio-temporal

57 variation in the density of a forest canopy can determine understorey light levels
58 (Parker et al. 2002), local climate and microclimate (Shuttleworth et al., 1989;
59 Clinton, 2003), tree regeneration (Barbeito et al., 2009; Bebber et al., 2002), plant
60 and animal community composition (Frelich et al., 2003; Richards and Windsor,
61 2007), and carbon storage (Penne et al., 2010). Quantifying canopy structure and
62 dynamics can therefore address critical questions in forest ecology (Lowman and
63 Rinker, 2004, Wilson 2011). We carried out a quantified analysis of canopy structure
64 as it related to land use history and recovery from active management, which could
65 add to current models of structural regeneration and thus guiding predictions about the
66 pace and direction of forest recovery from anthropogenic disturbance.

67 Forest canopies are highly dynamic, responding to disturbances across spatial
68 and temporal scales. Although forest successional dynamics cover a continuum of
69 disturbance intensity and frequency, natural mechanisms tend to lead to a limited
70 number of trajectories of canopy development observed across many types of
71 temperate broadleaf, close-canopy forests. Gap-phase dynamics are most commonly
72 associated with low-intensity, high-frequency disturbances, such as canopy openings
73 caused by the deaths of individual trees. The resulting small light gaps are filled
74 rapidly by advanced regeneration (i.e., juvenile trees that avoid the gap generating
75 disturbance) and ingrowth from neighbouring trees (Hubbell and Foster 1996; Brokaw
76 1999). Infrequent but high-intensity disturbances (e.g., wind throw, fire, liana-
77 connected tree-fall gaps) remove the canopy of large areas of forest, releasing tree
78 seedlings and saplings from competition for light, allowing incoming seeds to
79 colonize, thus initiating successional trajectories that are often predictable in terms of
80 canopy structure and vertical stratification and which play out across many decades or
81 centuries (Franklin et al., 2002; Ishii et al., 2004; Oliver and Larson, 1996).

82 Most temperate forests, however, are exposed to or recovering from
83 anthropogenic, rather than natural, disturbances, particularly from land use change
84 and timber management. Furthermore, the response to these disturbances may be
85 different where forest cover is highly fragmented as opposed to largely continuous
86 cover. For example, in the UK, forests have existed only as small isolated patches for
87 centuries due to human activities (FAO, 2010; Rackham, 2001; Whitney, 1996).

88 The recent availability of remote-sensing technologies offers the potential to make
89 accurate measurements of canopy structure, which allow us to explore different types
90 and intensities of anthropogenic disturbance on canopy structure.

91 LiDAR technology is a common approach to measuring forest structure (Wulder et
92 al., 2012). LiDAR systems use a range-finder to send and record the return of
93 many pulses of light per second, giving precise estimates of the distance of objects
94 from the source. LiDAR systems on aircraft or satellites can now provide information
95 on forest structure over landscapes and regional scales (Asner et al., 2012; Wulder et
96 al., 2012). Airborne systems, however, are expensive to build, maintain, and schedule
97 for specific studies. An alternative is to use a ground-based system, known as
98 Portable Canopy LiDAR (PCL) (Parker et al., 2004). This system is carried from a
99 front-facing platform at waist height and fires 2000 pulses/ second up through the
100 canopy rather than down on to it. This system captures 'slices' of the canopy instead
101 of 3-dimensional profiles, but it offers a precise, objective, and easily deployed
102 approach to measuring forest structure that is readily translatable to the similar class
103 of technologies used in airborne and satellite systems.

104 Here, we use a PCL system in forest fragments in the UK to determine if fragment
105 size, edge to core ratio, management history, and composition produce structural
106 patterns similar to those found in the forest successional stages (Fig. 1). Specifically,

we use PCL to test whether 1) woodland core differs in canopy structure from edge, and across fragments of varying sizes and shapes; 2) stand edges influences canopy structure; 3) forests that have been actively managed in the past follow successional recovery in the same way that forests that have grown up on open grazing land.

2. Materials and methods

2.1. Site

Field work was conducted at Wytham Woods, and the surrounding fragments in Oxfordshire, UK (1°20'W 51°47'N) in July and August 2009. Wytham Woods is a relatively large (ca. 400 ha) fragment of mixed woodland, surrounded by numerous other woodland fragments in an agricultural landscape matrix (Fig. 2), typifying the range of woodland sizes and management-histories found in the UK (Kirby and Gibson, 2010 and Supplement A). The wood is situated on a small hill rising to 165 m a.s.l. from the surrounding plain at 60 m a.s.l.

The Woods and fragments show a mixture of origins and management histories (Kirby and Gibson, 2010; Morecroft et al., 2008): ancient semi-natural woodland formerly treated as coppice; other semi-natural woodland regenerated naturally within former wood pasture or on open grazings, and plantations of both broad-leaves and conifers, some of were established on open ground and some within the ancient woodland. The semi-natural woodlands are mainly of National Vegetation Classification (Rodwell, 1991) type W8 (*Fraxinus excelsior* – *Acer Campestre* – *Mercurialis perennis*).

2.1.1 Permanent sample plots

Permanent sample plots were established in Wytham Woods and surrounding fragments in 2008 and 2009 (Table 1 and Fig. 2) (Supplement A). All stems above 1

131 cm diameter at 1.3 m height were tagged, mapped, identified to species, and diameter-
132 measured in the 18 ha Wytham core plot (Butt et al., 2009, Butt et al. 2014). In the
133 seven ‘satellite’ plots, the lower diameter at breast height (DBH) limit was 5 cm. The
134 satellite plots comprised two forest edge plots, and five plots in forest fragments of
135 differing sizes. In addition, five 100 m transects were established in the northern and
136 southern edges of Wytham Wood (Fig. 2).

137 Each plot was sampled by a series of transects (details in Table 1), totaling 4.5 km.
138 All transects were perpendicular to forest edges except the Southern Edge Fragment,
139 which is long and thin and had only one transect run lengthwise through it (Table 1).
140 The edge plots were sampled perpendicular to the forest boundary for ca. 100 m,
141 beginning 0–2 m from the boundary depending on whether dense, impenetrable
142 vegetation was present which could not be sampled (explained in Section 3).

143 *2.2 Portable Canopy LiDAR (PCL)*

144 Canopy structure data were collected from the plots along the transects using a
145 portable canopy LiDAR system (PLC). The PCL included an up-facing Riegl LD90-
146 3100VHS-FLP range-finder (Riegl USA, Orlando, Florida) attached with battery and
147 small note-book computer to a front-facing platform worn by the surveyor with a
148 harness system. The surveyor walked in a straight line at a consistent pace along the
149 transects, measuring the transects in subsections (5-30 m measurement paths,
150 depending on density of understorey vegetation). The rangefinder recorded distances
151 to nearest object at 2000 pulses/s (i.e. 2kHz of first returns). These returns were then
152 binned into 1 m² voxels, which can be thought of as vertically and horizontally
153 binned collections of beam returns, using 1 m bins. We accounted for the
154 tendency of lower objects to receive disproportionately more hits than higher objects
155 (because of occlusion by the lower objects) by applying the MacArthur-Horn

156 transformation to the combined returns for each voxel (MacArthur and Horn, 1969).
157 These transformed voxels results provide an estimate of the canopy height profile
158 (CHP), i.e. the variation in canopy density weith height above ground (Parker et al.,
159 2004) (Fig 1).

160 *2.3. Metrics and statistical analyses*

161 Because of the different units and structure of the data (where some metrics
162 integrate across a transect and others are indicated only by a column of voxels),
163 we conducted four types of analyses: first, we used bootstrapped transect data to
164 find site-differences in LiDAR derived metrics, analyzed the relationship between
165 metrics using mixed effect models where transects were nested within plots, we
166 used t-tests to examine edge effects, and regressed stem data (where available)
167 against site metrics using simple regression across plots. We also build canopy
168 height profiles to examine qualitative differences in comparison to abstracted
169 expectations.

170 Structural metrics describe the vertical and horizontal distribution of LiDAR returns
171 across sites (Parker and Russ, 2004; Parker et al., 2004) and the data for each vertical
172 column in each transect were summarized by the following metrics: Canopy height
173 h_{max} (m), mean highest recorded hit across a site (or the mean of the outer canopy);
174 Rugosity, R (unitless), the standard deviation of the outer canopy, describing the
175 roughness of the canopy surface (Parker and Russ, 2004); Canopy Area Index (CAI)
176 ($m^2 m^{-3}$) as the sum over all heights of the surface area of the canopy; Shannon's
177 diversity index H , a measure of evenness and occupancy in a column, calculated from
178 the values in each voxel up to h_{max} ; and E , the proportion of canopy below the
179 mean, which indicates skewness in the canopy. Statistical comparisons of these
180 metrics across sites were conducted by bootstrapping with replacement the voxel

columns at each site 1000 times (Nordman et al., 2007).

Significance tests of differences between plots in variables other than h_{med} and rugosity (which were site-wide variables and not transects nested in sites) were conducted using Generalized Linear Mixed Models fitted by Penalized Quasi-Likelihood (Venables and Ripley, 2002). Means were fitted for each site with autocorrelated Gaussian errors, and random intercepts for each transect. A correlation analysis of the columnar variables was conducted and Shannon's H was highly correlated with occupancy ($r = 0.83$), and so was excluded from analyses as occupancy is an easier variable to explain. Edge effects were tested by comparing canopy features in the 5, 10, and 15 m near an edge (when a transect met an edge) to the rest of the transect data using a t-test.

3. Results

There were clear differences in composition and structure between the different areas sampled but these were not obviously related to whether the areas were fragments, edge plots, or core (Tables 1 and 2), although the Northern Edge and Wytham Core did show greater mean height of the outer canopy and canopy occupancy (Fig. 3). When height was taken into account (as through the use of the E Ratio, Wytham Core showed a similarly skewed profile (E_Ratio in Fig. 3) as most other sites (a notable exception being Wood Decay North). Wytham Core also showed high diversity of canopy structure, and North Edge showed greater Rugosity than the other sites.

The only clear difference between the sites was in CAI, which was greater, and less variable, in the Southern than the Northern transects and rugosity, which was higher in the Northern Edge. The Core had the tallest canopy, but h_{max} was not significantly

greater than that of the Northern Edge, which had the next-tallest canopy (mean 15.19 ± 0.40 m vs. 15.16 ± 0.62 m, $t = 0.05$, $df = 33$, $p = 0.96$). CAI and Occupancy did not differ markedly among sites (Fig. 3), but rugosity was significantly higher in the Northern Edge compared with the other sites (t-test of Northern Edge median vs. other sites, $t = 11.3$, $df = 8$, $p < 10^{-5}$). In the correlation analysis, basal area was not correlated with any structure metrics.

There were negative relationships between h and the density of tree stems from surveys. This is due to the fact that stem diameter varies negatively with stem density, and positively with tree height. As stands mature, the many initiating stems thin, while the winners grow taller and wider. The negative relationship between rugosity and stem density appears largely due to the Northern Edge plot, which has a tall canopy of similarly sized large ash and relatively few canopy gaps.

LiDAR-derived metrics revealed that although there were differences among areas in a number of characteristics there were no clear edge effects at either 5, 10 or 15 m), independent of fragment size or composition ($p > 0.05$ in all tests). Thus, where a transect ended at the edge of the forest stand, there were no clear or unique structural features at the transects end compared to areas just before the end. The only features not captured in this analysis, where edges clearly were important, were edges with thick brambles bordering an adjacent open field (i.e., ‘sealed’ edges). These prohibited measurement, as they were impassable, but the brambles did not extend into the forest or influence forest structure beyond several meters on any transect.

As with canopy height, the canopy height profiles (CHP, which show the vertical distribution of vegetation at each site (Fig. 4)) showed again that the two sites that had the least active management histories (Wytham Core [WC] and the

230 Northern Edge [NE] (Supplement)) had a qualitatively different canopy structure
231 compared with the other sites (Fig. 4, results detailed above). The WC CHP was
232 strongly bimodal, with density peaks at 6 m and 16 m. This bimodal distribution
233 was not evident in any of the other plots, which have a single mode at 5–8 m, and
234 declining density at greater heights.

235 4. Discussion

236 Forest stands can differ dramatically in vegetation structure and this was detectable
237 using the ground-based LiDAR system. Most methods of remote sensing of forest
238 structure over large extents are achieved through airborne or satellite LiDAR. There
239 have been extensive studies that ground-truthing can work in relatively undisturbed
240 locations. However, few forests have the variety of past land use and depth of
241 knowledge of this use as Wytham Woods. This LiDAR study takes advantage of
242 the focused approach to quantifying the complete vertical structure of stands
243 offered by the PCL method, as well as the extensive history and variety of those
244 measured stands, to investigate whether stand location and fragment size show
245 consistent features independent of historical use and how structural patterns match
246 historical and compositional patterns.

247 No evidence was found for edge effects on canopy structure, either among
248 plots or within edge transects. The UK has 12% forest cover (>0.1 ha), and this is
249 highly fragmented with 75% of all woodland parcels being in the range 0.1–2
250 ha, (Forestry Commission, 2003). Small woodlands (<50 ha) make up 51% of
251 total forest area, and therefore edge effects are thought to be pervasive (Riutta et
252 al., 2014). This makes the lack of apparent edge effects on canopy structure
253 surprising, but perhaps explained by the highly idiosyncratic nature of forest
254 edges (Harper et al., 2005). Wytham has a maintained edge (i.e. there is an

255 anthropogenic boundary between forest and non-forest), thereby causing the
256 development of a ‘side-wall’ of dense, shrubby vegetation that ‘seals’ the edge
257 against ingress of wind and sunlight, and thereby obviates any edge effects of
258 structure further inside the understory (Harper et al., 2005). Indeed, we could
259 not sample the outer boundary of many of the edge transects due to the high
260 density of impenetrable blackthorn (*Prunus spinosa*) and bramble (*Rubus*
261 *fruticosus*). This, of course, does not indicate a lack of edge effects on the
262 ecology or composition of the forest, merely the structure. Given the impor-
263 tance of historical uses of fragmented forests, it is possible to think of legacies of
264 those histories as the more dominant ‘edge effect’ than the transition zones in
265 the forest near open fields.

266 Land use and management history may provide an alternative explanation for the
267 differences between the areas sampled. In the Supplement, we describe in greater detail
268 the differences between site histories. We found a clear pattern related to canopy
269 structure which distinguished among management types, rather than time since
270 management. Coppiced trees lead to a unique canopy structure that tends to be short,
271 dense, and with more uniform composition, even after decades of protection. Wytham
272 Core and the Northern Edge, both with less active management histories than other
273 sites, also have taller heights than other sites. Even when influenced by invasion, such
274 as sycamore presence in Wytham Core, height profiles (both maximum and median
275 height) show a clear difference from sites that have been used for coppicing, even
276 if many decades ago.

277 Wytham Great Wood, the site of the Core plot, has a high density of sycamore,
278 which appears to have invaded the disturbed woodland. This in contrast to the ancient
279 semi-natural woodlands on the lower slopes at Wytham (Morecroft et al., 2008).

280 Sycamore is known for its ability to invade open sites with little overstorey or ground-
281 level competition (Hein et al., 2009), so perhaps sycamore succeeded in colonizing
282 gaps in the Wytham Core created by the deaths of large ancient oaks. The fact that
283 even with an invasive pioneer, such as sycamore, the CHP of Wytham Core still
284 appears similar to old growth forest (Perker and Russ, 2004) indicates the difficulty in
285 determining forest composition from structure.

286 The high density of ash seen in the Northern Edge plot also indicates significant
287 historical spread out from the wood on to former grazing land (albeit with some
288 scattered trees) from which the animals had been withdrawn; ash commonly
289 establishes in disturbed sites both through dispersal of its winged fruit, and by
290 vegetative ingrowth and persistence of stumps (Marigo et al, 2000). Management
291 plans for Wytham from the 1950s point to another cohort of ash establishing at that
292 time on former grassland after the decline of the rabbit population (Kirby and
293 Gibson, 2010). This composition, however is likely to change in the next decade due
294 to the impending introduction into Wytham of ash dieback disease
295 (*Hymenoscyphus pseudoalbidus* V. Queloz (Pautasso et al., 2013)). With upwards
296 of 90% mortality, we expect a significant shift in species composition, and also in
297 canopy structure over the next decade.

298 The distribution of foliage towards the lower canopy seen in Higgins, Bean Wood and
299 the Southern Edge Fragment might suggest that these are mature forest, in which a
300 shade tolerant understorey is developing. However, these areas are known to have a
301 long history of coppice management with “standards” (i.e. a number of oak trees left
302 to mature for use as timber) (Kirby and Gibson, 2010). The remnant coppice stools,
303 primarily of ash, field maple and hazel, comprise the understorey, while the standards
304 make up the overstorey. Rather than being recent arrivals, some of the coppices are

likely the oldest living organisms in Wytham (Kirby and Gibson, 2010), even though the stems growing from them are quite young.

5. Conclusions

Airborne and space-borne LiDAR are increasingly important tools for characterising forest structure and process over vast regions (Asner et al., 2012; Frohking et al., 2009; Lefsky et al., 2002; Wulder et al., 2012). Although an important component of this monitoring focuses on estimating above-ground biomass using allometries and stand height, in an increasingly large part of the world, forests will not have the allometries shown by undisturbed forest stands. Instead, recovering forests around the world will show the structural legacies of human use due to timber harvest, silviculture, the influx of invasive species, hunting, and other effects, such as coppicing. As ground-truthing remotely-sensed data is essential to validating and interpreting inferred structural variables, we demonstrate here that a new kind of ground-truthing might be required for global assessments of forest health. We show that there is a risk of misinterpreting canopy height profiles if the disturbance history (both natural and anthropogenic) is not understood. Portable canopy LiDAR provides a convenient, inexpensive and robust tool to bridge the gap between forest inventories and remote sensing, especially if we are to take into account the myriad ways in which humans interface with forests. For global extrapolations of LiDAR-detected vegetation structure, especially when these data will be used to predict trajectories of future structure, we must consider the diverse modes and intensities of disturbance and management within the scope of the classic remote-sensing validation process.

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330 **References**

- 331 Asner, G.P., Knapp, D.E., Boardman, J., Green, R.O., Kennedy-Bowdoin, T.,
332 Eastwood, M., Martin, R.E., Anderson, C., Field, C.B., 2012. Carnegie
333 Airborne Observatory-2: Increasing science data dimensionality via high-
334 fidelity multi-sensor fusion. *Remote Sensing of Environment* 124, 454–465.
- 335 Barbeito, I., Fortin, M.-J., Montes, F., Cañellas, I., 2009. Response of pine natural
336 regeneration to small-scale spatial variation in a managed Mediterranean
337 mountain forest. *Applied Vegetation Science* 12, 488–503.
- 338 Bebber, D., Brown, N., Speight, M., Moura-Costa, P., Wai, Y.S., 2002. Spatial
339 structure of light and dipterocarp seedling growth in a tropical secondary
340 forest. *Forest Ecology and Management* 157, 65–75.
- 341 Brokaw, Nicholas V.L., 1985. Gap-phase regeneration in a tropical forest.
342 *Ecology* 66, 682–687.
- 343 Butt, N., Campbell, G., Malhi, Y., Fenn, K., Thomas, M., 2009. Initial results from
344 establishment of a long-term broadleaf monitoring plot at Wytham Woods,
345 Oxford, UK. University of Oxford, Oxford, UK.
- 346 Clinton, B.D., 2003. Light, temperature, and soil moisture responses to elevation,
347 evergreen understory, and small canopy gaps in the southern Appalachians.
348 *Forest Ecology and Management* 186, 243–255.
- 349 FAO, 2010. Global Forest Resources Assessment 2010 (FAO Forestry Paper No.
350 163). Food and Agriculture Organization of the United Nations, Rome.
- 351 Forestry Commission, 2003. Great Britain national inventory of woodland and trees.
352 Forestry Commission, Edinburgh.

353 Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R.,
 354 Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K.,
 355 Chen, J., 2002. Disturbances and structural development of natural forest
 356 ecosystems with silvicultural implications, using Douglas-fir forests as an
 357 example. *Forest Ecology and Management* 155, 399–423.

358 Frelich, L.E., Machado, J.-L., Reich, P.B., 2003. Fine-scale environmental variation
 359 and structure of understorey plant communities in two old-growth pine forests.
 360 *Journal of Ecology* 91, 283–293.

361 Froking, S., Palace, M.W., Clark, D.B., Chambers, J.Q., Shugart, H.H., Hurtt, G.C.,
 362 2009. Forest disturbance and recovery: A general review in the context of
 363 spaceborne remote sensing of impacts on aboveground biomass and canopy
 364 structure. *J. Geophys. Res.* 114, G00E02.

365 Harper, K.A., MacDonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders,
 366 S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Esseen, P.-A., 2005. Edge
 367 Influence on Forest Structure and Composition in Fragmented Landscapes.
 368 *Conservation Biology* 19, 768–782.

369 Hein, S., Collet, C., Ammer, C., Goff, N.L., Skovsgaard, J.P., Savill, P., 2009. A
 370 review of growth and stand dynamics of *Acer pseudoplatanus* L. in Europe:
 371 implications for silviculture. *Forestry* 82, 361–385.

372 Hubbell, S.P., Foster, R.B., 1986. Biology, chance and history and the structure of
 373 tropical rain forest tree communities. In: Diamond, J., Case, T.J. (Eds.),
 374 *Community Ecology*. Harper and Row, New York, pp. 314–329 (Chapter
 375 19)

376 Ishii, H.T., Van Pelt, R., Parker, G.G., Nadkarni, N.M., 2004. Age-related

377 development of canopy structure and its ecological functions, in: Lowman,
 378 M.D., Rinker, H.B. (Eds.), *Forest Canopies*. Elsevier Academic Press,
 379 Burlington, MA, pp. 102–117.

380 Kirby, K.J., Gibson, C.W.D., 2010. The Woods in the modern landscape, in: Savill,
 381 P.S., Perrins, C.M., Kirby, K.J., Fisher, N. (Eds.), *Wytham Woods: Oxford's*
 382 *Ecological Laboratory*. Oxford University Press, Oxford, pp. 43–56.

383 Lefsky, M.A., Cohen, W.B., Parker, G.G., Harding, D.J., 2002. Lidar remote sensing
 384 for ecosystem studies. *BioScience* 52, 19–30.

385 Lowman, M.D., Rinker, H.B. (Eds.), 2004. *Forest Canopies*. Academic Press.

386 MacArthur, R.H., Horn, H.S., 1969. Foliage Profile by Vertical Measurements.
 387 *Ecology* 50, 802–804.

388 Marigo, G., Peltier, J.-P., Girel, J., Pautou, G., 2000. Success in the demographic
 389 expansion of *Fraxinus excelsior* L. *Trees* 15, 1–13.

390 Morecroft, M.D., Stokes, V.J., Taylor, M.E., Morison, J.I.L., 2008. Effects of climate
 391 and management history on the distribution and growth of sycamore (*Acer*
 392 *pseudoplatanus* L.) in a southern British woodland in comparison to native
 393 competitors. *Forestry* 81, 59–74.

394 Nordman, D.J., Lahiri, S.N., Fridley, B.L., 2007. Optimal block size for variance
 395 estimation by a spatial block bootstrap method. *Sankhyā: The Indian Journal*
 396 *of Statistics* 69, 468–493.

397 Oliver, C.D., Larson, B.C., 1996. *Forest stand dynamics*, 2nd ed. Wiley.

398 Parker, G.G., Harding, D.J., Berger, M.L., 2004. A portable LIDAR system for rapid
 399 determination of forest canopy structure. *Journal of Applied Ecology* 41, 755–

400 767.

401 Parker, G.G., Russ, M.E., 2004. The canopy surface and stand development: assessing
402 forest canopy structure and complexity with near-surface altimetry. *Forest*
403 *Ecology and Management* 189, 307–315.

404 Pautasso, M., Aas, G., Queloz, V., Holdenrieder, O., 2013. European ash
405 (*Fraxinus excelsior*) dieback – a conservation biology challenge. *Biol.*
406 *Cons.* 158, 37–49.

407 Penne, C., Ahrends, B., Deurer, M., Böttcher, J., 2010. The impact of the canopy
408 structure on the spatial variability in forest floor carbon stocks. *Geoderma* 158,
409 282–297.

410 Rackham, O., 2001. *Trees and Woodland in the British Landscape*, 2nd ed. Phoenix.

411 Richards, L.A., Windsor, D.M., 2007. Seasonal variation of arthropod abundance in
412 gaps and the understorey of a lowland moist forest in Panama. *Journal of*
413 *Tropical Ecology* 23, 169–176.

414 Riutta, T., Slade, E.M., Morecroft, M.D., Bebbier, D.P., Mahli, Y., 2014. Living
415 on the edge: quantifying the structure of a fragmented forest landscape in
416 England. *Landscape Ecology* 29 (6), 949–961.

417 Rodwell, J.S. (Ed.), 1991. *British Plant Communities*. Cambridge University Press.

418 Shugart, H.H., Saatchi, S., Hall, F.G., 2010. Importance of structure and its
419 measurement in quantifying function of forest ecosystems. *J. Geophys. Res.*
420 115, G00E13.

421 Shuttleworth, W.J., Leuning, R., Black, T.A., Grace, J., Jarvis, P.G., Roberts, J.,
422 Jones, H.G., 1989. *Micrometeorology of Temperate and Tropical Forest*. Phil.

423 Trans. R. Soc. Lond. B 324, 299–334.

424 Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, 4th ed.

425 Springer, New York.

426 Whitney, G.G., 1996. From Coastal Wilderness to Fruited Plain: A History of

427 Environmental Change in Temperate North America from 1500 to the Present.

428 Cambridge University Press.

429 Wilson, J.B., 2011. Cover plus: ways of measuring plant canopies and the terms used

430 for them. *Journal of Vegetation Science* 22, 197–206.

431 Wulder, M.A., White, J.C., Nelson, R.F., Næsset, E., Ørka, H.O., Coops, N.C.,

432 Hilker, T., Bater, C.W., Gobakken, T., 2012. Lidar sampling for large-area

433 forest characterization: A review. *Remote Sensing of Environment* 121, 196–

434 209.

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437 Tables

438 Table 1. Plot summary. Type refers to whether the plot is in a forest fragment
 439 (“Frag”), on the edge of Wytham Woods (“Edge”) or in the center of Wytham
 440 Woods (“Core”). These are all designated research plots, and not stands. Area is
 441 the total area of the woodland contiguous to the plot. Plot is the area of the plot.
 442 Trans is the total number of PCL transects sampled. Length is the total length of
 443 those combined transects. Stems is the density of stems >5 cm DBH in the plot.
 444 BA is the basal area of those stems. Oaks is the density of large (>70 cm DBH)
 445 oak trees in the plot.

Plot	Type	Area (ha)	Plot (ha)	Trans	Length (m)	Stems (ha ⁻¹)	BA (m ² ha ⁻¹)	Oaks (ha ⁻¹)
Bean Wood	Frag	21.7	1.0	5	680	1505	29.5	10.0
Higgins	Frag	4.8	1.0	3	413	1202	30.8	8.0
North Edge	Edge	361.0	0.96	9	540	854	36.8	3.1
South Edge	Edge	361.0	0.96	1	112	1049	31.8	11.5
South Edge Frag	Frag	0.4	0.32	7	420	1525	38.4	31.3
Stimpsons	Frag	1.2	0.48	3	271	1392	40.7	16.7
Stroud	Frag	9.3	1.0	3	568	1298	38.5	13.0

Wytham Core	Core	361.0	18.0	3	1500	1128	33.3	5.2
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447 Table 2. Basal area of major species from plot inventory ($\text{m}^2 \text{ ha}^{-1}$). These species

448 make up > 90 % of the basal area in each of the plots.

Plot	Oak	Ash	Sycamore	Hazel	Field maple	Hawthorn
Bean Wood	16.8	3.8	0.0	5.1	1.6	0.4
Higgins	6.1	11.3	0.0	9.9	2.5	0.2
North Edge	5.2	24.0	0.0	1.4	2.6	3.2
South Edge	8.2	12.5	0.0	0.9	7.0	1.5
South Edge Frag	29.8	0.0	0.0	0.0	0.3	4.1
Stimpsons	16.9	12.3	0.1	7.8	0.6	0.4
Stroud	13.6	9.3	0.0	1.1	11.1	3.0
Wytham Core	6.7	6.7	16.9	0.4	0.2	0.3

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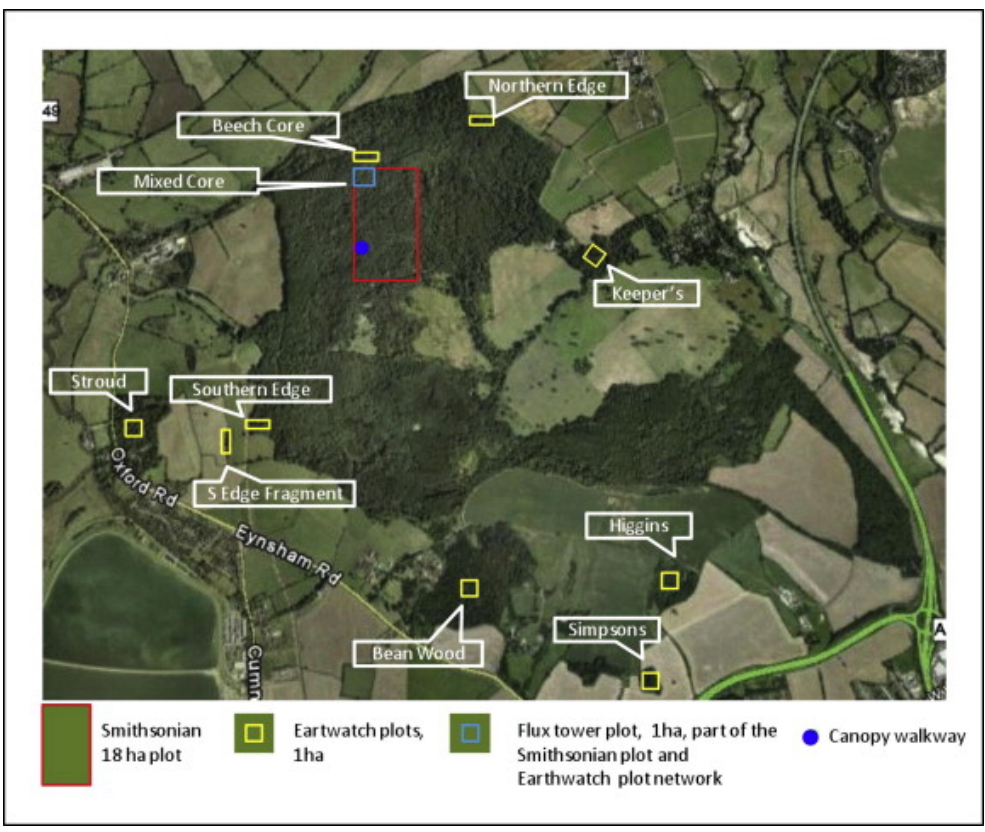
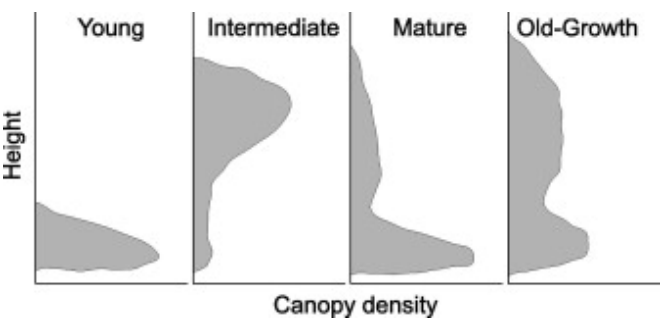
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452 **Figures**

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455 Fig. 1. Abstracted Canopy Height Profiles (CHPs) for Young, Intermediate, Mature
456 and Old-Growth forest stands in the Eastern USA (adapted from Parker and Russ
457 (2004)). Although initial stand formation shows dense, uniform canopy with little
458 understorey, as the forest matures, treefall gaps allow a mix of over and understorey
459 vegetation. Stand maturity in this successional pathway also leads to higher outer
460 canopy.



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462 Fig. 2. Map of Wytham Woods core and fragments.

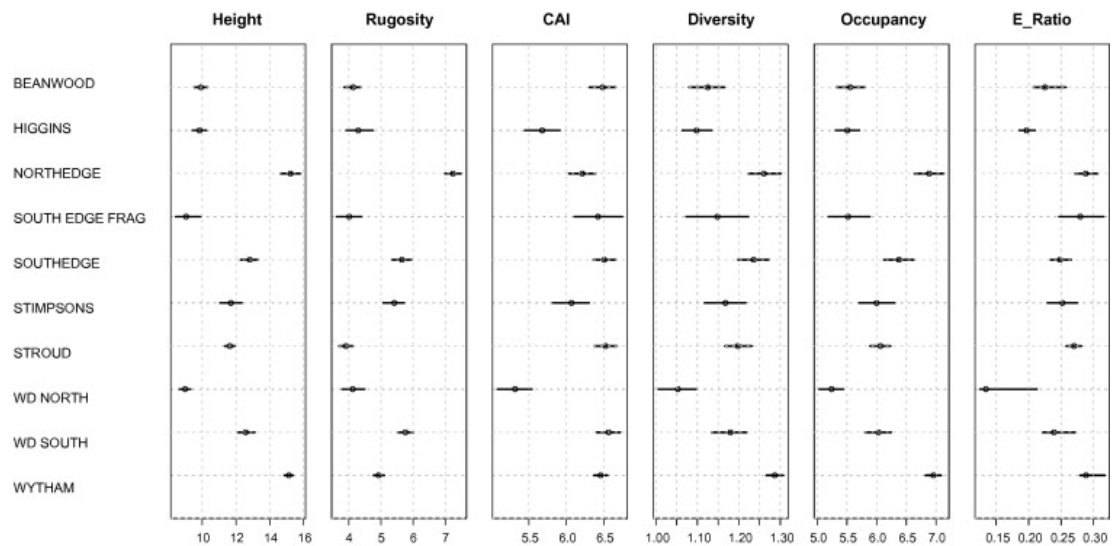


Fig. 3. Bootstrapped comparisons of canopy metrics across all sites. 1000 replicate ‘plots’ were simulated. Dots show the median values from the simulations and lines show the 0.025 and 0.975 quantiles of the bootstrapped values.

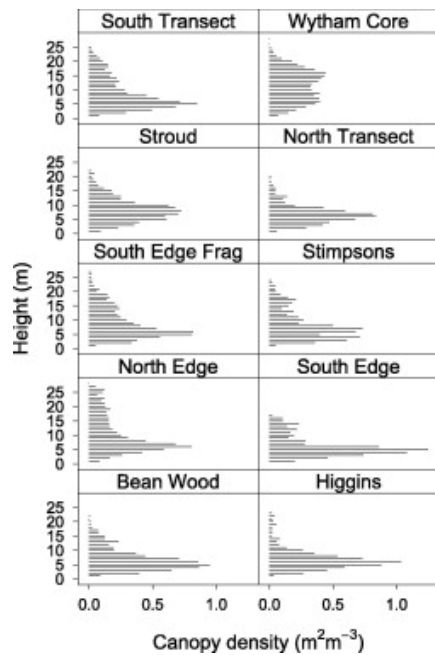


Fig. 4. Canopy Height Profiles for PCL measurements in the studied plots and fragments. Although the Wytham Core and North Edge show the expected ‘mature’ stage of forest succession, most fragments show CHPs that are shorter than mature forest, but contain significant understorey.